DUNGENESS CRAB, *CANCER MAGISTER*, DO NOT EXTRUDE EGGS ANNUALLY IN SOUTHEASTERN ALASKA: AN *IN SITU* STUDY

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ABSTRACT

The reproductive biology of female Dungeness crabs was studied with crab-pot and dive-transect sampling in five bays within or near Glacier Bay National Park and Preserve, southeastern Alaska, in April and September yearly from 1992 to 1998. A large percentage of nonovigerous, mature females was found in April, a time when females were expected to be brooding eggs that hatch in May and June. Our study examined differences between ovigerous and nonovigerous females collected in April and September samples to corroborate our previous laboratory study in which we found nonannual egg extrusion among Dungeness crabs. Seasonal differences in the catches of ovigerous and nonovigerous females, crab sizes, shell condition, and appendage injury were examined. Additionally, all crabs collected from two bays were tagged beginning in the fall of 1995; tagging was conducted twice annually. Our pot and dive data indicate that females, particularly larger ones, do not extrude eggs annually. Larger females have lower molting probabilities, which limits mating potential and increases reliance on stored sperm. The tagging study confirmed that at least some females do not extrude eggs in one year and then extrude eggs at a later time without molting, thus skipping at least one reproductive season. A reproductive cycle of Dungeness crabs in Alaska is introduced which includes earlier egg extrusion by larger females and nonannual egg extrusion.

Dungeness crabs (*Cancer magister* Dana 1852) support important commercial fisheries from central California to Kodiak, Alaska. To effectively manage this species, basic knowledge of Dungeness crab reproduction and life history is necessary.

Mating in *Cancer magister* occurs between hard-shelled males and recently molted females that are in a soft-shelled condition (MacKay, 1943; Butler, 1960; Snow and Neilsen; 1966). Sperm is stored in paired spermathecae, and eggs are fertilized as they pass by the spermathecae during extrusion (Jensen *et al.*, 1996). Dungeness crabs can store and utilize sperm for at least 2.5 years (Hankin *et al.*, 1989). Dungeness crabs in southeastern Alaska begin mating in June and July (Stone and O'Clair, 2001) and extrude eggs August through January (Swiney, 1999; Swiney and Shirley, 2001). Eggs hatch April through August with most of the hatching occurring in May and June (Shirley *et al.*, 1987; Swiney,

1999; Stone and O'Clair, 2001; Swiney and Shirley, 2001).

Dungeness crabs are generally thought to extrude eggs annually (Jaffe *et al.*, 1987; Shields, 1991), but evidence has recently been presented that not all mature female Dungeness crabs in southeastern Alaska extrude eggs annually (Swiney and Shirley, 2001). Alaska is the northern range limit for Dungeness crabs (Hart, 1982), and this may affect the periodicity of reproduction.

If all mature females were extruding eggs annually, a high percent of ovigerous females would be expected in the spring. However, only sixty-seven percent of mature females collected throughout southeastern Alaska during May 1982 and April 1983 were ovigerous (O'Clair and Freese, 1988). Divers collected the female crabs by swimming along approximately parallel tracks in a ladder search (O'Clair and Freese, 1988). Similar results were obtained in a laboratory study in which a large percentage of

Table 1. Sampling dates for yearly spring and fall pot and dive surveys for Dungeness crabs in Glacier Bay National Park and Preserve, Alaska.

	Spring Sampling		Fall Sampling	
	Pot	Dive	Pot	Dive
1992	April 7–12	April 7–12	Sept. 17–22	Sept. 17–22
1993	April 20–27	April 20–27	Sept. 23–28	Sept. 23–28
1994	April 20–27	April 25–May 1	Sept. 13–18	Sept. 13–18
1995	April 19–26	April 25–May 1	Sept. 9–14	Sept. 15–19
1996	April 15–21	April 22–28	Sept. 13–18	Sept. 19–23
1997	April 17–22	April 23–28	Sept. 14–19	Sept. 20–25
1998	—	—	Sept. 9–14	Sept. 17–22

females did not extrude eggs while in captivity for over a year (Swiney and Shirley, 2001). The same laboratory study compared gonadosomatic indexes and oocyte areas of ovigerous females with those that were nonovigerous when collected and concluded that many mature female Dungeness crabs in southeastern Alaska do not extrude eggs annually (Swiney and Shirley, 2001).

Data from a multiyear study were combined and analyzed to determine whether the conclusions of Swiney and Shirley (2001), that some females do not extrude eggs annually, would be confirmed in the field, and to shed added light on the periodicity of egg extrusion in Dungeness crabs. In this study, we specifically: 1) examined the effects of pot and dive-transect sampling and season on the numbers of nonovigerous and ovigerous female encountered; 2) compared sizes of nonovigerous and ovigerous females seasonally; 3) determined whether the frequency of a female having one or more appendages damaged, missing, or regenerating was independent of female reproductive condition; 4) examined shell condition of nonovigerous and ovigerous females seasonally.

MATERIALS AND METHODS

The study area included five bays in southeastern Alaska. Four of the bays—north Beardslee Islands (58°31′N, 135°54′W), south Beardslee Islands (58°30′N, 135°53′W), Berg Bay (58°31′N, 136°13′W), and Bartlett Cove (58°27′N, 135°53′W)—are located within Glacier Bay National Park and Preserve. The fifth bay, Gustavus Flats (58°23′N, 135°43′W), is adjacent to the park's boundary.

Sampling was conducted biannually in April (spring) and September (fall) (Table 1). These sampling periods were selected to avoid conflicts with the commercial fishery and to coincide with reproductive events of Dungeness crabs (Swiney and Shirley, 2001). April sampling occurred prior to egg hatching, which usually occurs in May and June, and before the commercial fishery opens in June. September sampling occurred during a time of mating and egg extrusion and when the commercial fishery is closed from August 15th to September 30th. Data were pooled from five

bays and analyzed seasonally from the initiation of the project in April 1992 to September 1998; no sampling occurred in April of 1998 (Table 1).

Commercial crab pots were used for crab collection. Pots were baited with fresh hanging bait of halibut, salmon, or cod and perforated bait jars containing chopped squid and herring. Five bays were fished with 50 pots each for 24 hours on five consecutive days. The pot mesh had 5-cm stretched diamond-shaped openings, and the escape rings of the pots were sealed with webbing to retain smaller crabs. Approximately half of the pots were set between 0 and 9 m depth, and half were set between 10 and 25 m. Pots were placed parallel to the shore. The location, set and retrieval times, and depth were recorded for each pot. The same pot positions were used each sampling period by employing a portable military Global Positioning System unit (Rockwell PLGR$^+$) with an accuracy of $\pm$ 3 m to relocate the correct positions.

All species collected in the pots were counted and recorded. Dungeness crabs were examined further by sex, size (carapace width), shell condition, appendage injury, and reproductive condition. Female Dungeness crabs were recorded as either ovigerous or nonovigerous. Carapace width (CW) was measured to the nearest millimeter immediately anterior to the tenth anterolateral spine with vernier calipers. Shell condition was determined by appearance and hardness: soft shells were soft to the touch; new shells had sharp spines, were bright in color, and free of fouling organisms; old shells had dull spines, were not as bright in color, and had some fouling organisms; and very old shells had very dull spines and color, and had fouling organisms (Shirley and Shirley, 1988). Injury was recorded as missing, damaged, or regenerating for each appendage. Carapace damage was also recorded. Females were examined for the presence of blackened pleopods. The setae and pleopods of female crabs can become blackened after eggs have hatched; the organic matter remaining from egg cases is chemically reduced and smells strongly of hydrogen sulfide. The condition of blackened pleopods can be used as an indicator of recent female reproductive history because a female would have blackened pleopods only if she had brooded eggs and had not molted. Females may or may not always produce or retain blackened pleopods after egg hatching and until molting (Swiney, 1999). In this study, blackened pleopods were observed only in the fall samples. Cleaning of pleopods has been suggested for *Cancer gracilis* Dana, 1852 (Orensanz *et al.*, 1995), and occurs in some laboratory-reared Dungeness crabs (T. Shirley, unpublished observations). Because it is not known how long blackened pleopods persist, a conservative interpretation was used in analyzing our data. The presence of blackened pleopods was interpreted as evidence of recent egg brooding

and no molting, but the absence of blackened pleopods was not evidence for a lack of recent brooding.

Crabs were also sampled along dive transects in each bay. Transects 2 m × 100 m in the depth range of 0 (mean lower low water) to 18 m were established perpendicular to shore. Some transects were less than 100 m long because the depth limit was reached before the end of the transect. Transects were positioned randomly or systematically near pot locations. Usually 20 dive transects were conducted in each bay during each sampling period. Numbers of males, nonovigerous, and ovigerous female crabs were recorded, including crabs buried, but visible on the transects. The crabs encountered on transects were not measured. No crabs were collected for this study unless a tagged crab was encountered (see below), in which case the divers would collect it temporarily to record the tag number, measure the carapace width, and record any observations that may give insight into her history since being tagged. These crabs were released alive at their collection site.

Beginning in fall 1995, all crabs caught in crab pots and ovigerous females encountered by divers in South Beardslee Islands and Berg Bay were tagged with 7.6-cm double-T Floy tags. The tags, designed to remain attached through molting, were positioned on the right posterior epimeral line near the branchial chamber. Each tag had data identifying the project and a unique number. A total of 1739 females were tagged: 1427 were nonovigerous, and 312 were ovigerous.

A saturated loglinear model was used to determine the effects of sampling type (pot and dive transects), season, and the number of females caught by female reproductive condition (nonovigerous and ovigerous). Fall 1998 data were not included in the analysis because there were no spring 1998 data with which to pair (Table 1). Partial associations were reported for each of the main and interaction effects in the model.

To determine whether significant differences occurred between female reproductive condition, season, and carapace width, a 2-way ANOVA was conducted using pot data pooled over all the years of data. The main effects of reproductive condition and season were included in the analysis as well as the interaction term for reproductive condition and season.

For pot data, Fisher's exact test of independence was used to examine whether the frequency of a female having one or more appendages damaged, missing, or regenerating was independent of female reproductive condition. Data were examined by season, and data were pooled over all of the years of the study. Three separate analysis were conducted, one for each of the appendage injuries.

Potential effects of carapace condition on female reproductive condition were tested seasonally using G tests. Pot data were combined over the years of the study in this analysis. Soft-shelled ovigerous females were not caught; therefore, the soft-shell condition was not included in the analyses.

Data on the reproductive condition, size, and presence of blackened pleopods of recaptured female crabs were compared to the data collected when they were initially captured to reconstruct reproductive activity for individual crabs. If a female increased in size, we assumed that she had molted since tagging. If a female had not molted between captures and had blackened pleopods in the fall, we assumed that she brooded a clutch the previous spring. Likewise, if a nonovigerous female was caught in the spring, we assumed that she did not brood eggs that year. If a female molted between when she was tagged and recovered and was nonovigerous when recovered, her recent reproductive
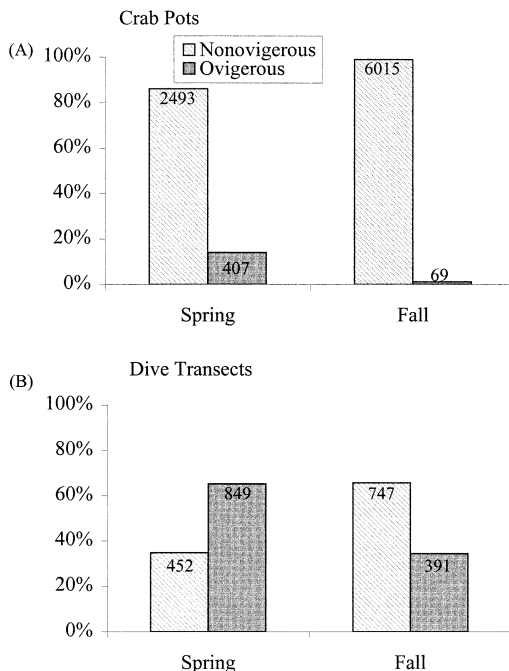

Fig. 1. Comparison of the percentage of nonovigerous and ovigerous female Dungeness crabs caught in crab pots (A) or observed on dive transects (B) in spring and fall. Six spring samples and seven fall samples are represented.

history was ambiguous because she would have shed the blackened pleopods (if they were present) during the molt.

Statistics were calculated using SPSS Advanced Models 10.0 (1999), StatView (1996), and by methods described in Sokal and Rohlf (1995). Values were considered significant when $P < 0.05$ and highly significant when $P < 0.001$.

RESULTS

A total of 27,506 crabs were sampled in this study. The crab pots yielded 8508 nonovigerous females, 476 ovigerous females, and 14,537 males. The size of females caught in crab pots ranged 100–190 mm carapace width (CW) for nonovigerous females and 106–180 mm CW among ovigerous females. On dive transects, 1199 nonovigerous females, 1240 ovigerous females, and 1546 males were sampled (Fig. 1). These catches may not represent true population percentages of males, nonovigerous and ovigerous females because of sampling biases (Howard, 1982; O'Clair et al., 1990; Taggart et al., in review).

We observed interactions between sampling method, season, and numbers of nonovigerous and ovigerous females caught. A difference was detected for the main effects of sampling type (Partial $\chi^2 = 3988.2$, $P < 0.0001$), season
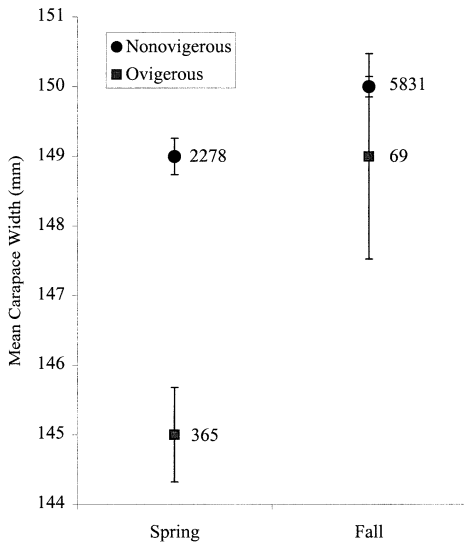
Fig. 2. Mean carapace widths of ovigerous and non-ovigerous female Dungeness crabs with respect to season. Values are mean ± one standard error.

(Partial $\chi^2 = 808.5$, $P < 0.0001$), and female reproductive condition (Partial $\chi^2 = 6169.6$, $P < 0.0001$). More crabs were caught in crab pots than were encountered by divers swimming transects; more females were encountered in the fall samples than in the spring, and more nonovigerous than ovigerous females were caught overall (Fig. 1). A difference was detected between sampling type and female reproductive condition (Partial $\chi^2 = 2209.8$, $P < 0.0001$). More nonovigerous than ovigerous females were caught in crab pots. Conversely, more ovigerous than nonovigerous females were encountered on dive transects (Fig. 1). An interaction was detected for sampling season and female reproductive condition (Partial $\chi^2 = 764.8$, $P < 0.0001$). More ovigerous females were caught in the spring than in fall samples, and more nonovigerous females were caught in the fall samples than in the spring samples (Fig. 1). A difference was not detected for the interaction of sampling type and season (Partial $\chi^2 = 3.0$, $P > 0.05$). The pot and dive sampling encountered ovigerous females in April; however, if all mature females extrude eggs annually, one would expect nearly all of the females encountered in the spring to be ovigerous.

Carapace width differed between nonovigerous and ovigerous females ($F = 12.4$, $P < 0.001$) and between spring and fall samples ($F = 7.0$, $P < 0.01$). The interaction of season and female reproductive condition did not have

an influence on carapace width ($F = 2.1$, $P > 0.05$). In the spring samples, nonovigerous females ($\bar{x} = 149.3 \pm 0.3$ mm) were approximately 4 mm larger than ovigerous females ($\bar{x} = 145.4 \pm 0.7$ mm) (Fig. 2). In the fall samples, nonovigerous females were only slightly larger ($\bar{x} = 150.2 \pm 0.1$ mm) than ovigerous females ($\bar{x} = 148.6 \pm 1.5$ mm) (Fig. 2). Larger females may have extruded eggs earlier in the reproductive season and were collected as ovigerous in the fall samples. The observed decrease in the size of ovigerous crabs in the spring may have resulted from smaller females extruding eggs after the fall sampling.

The frequency of females with one or more damaged, missing, or regenerating appendages was examined for independence with respect to female reproductive condition and season. Comparisons were made using crab-pot data combined from all years. In the spring samples, a higher proportion of ovigerous females than nonovigerous females had one or more damaged appendages (Fisher's Exact $P < 0.0001$, Fig. 3). In the fall, the proportions of non-ovigerous and ovigerous females with one or more appendages damaged did not differ (Fisher's Exact $P > 0.05$, Fig. 3). The frequency of females with one or more missing or regenerating appendages was independent of female reproductive condition and season. Damaged, missing, and regeneration of appendages does not appear to inhibit female egg extrusion. The higher appendage damage observed among ovigerous females in the spring samples may have occurred during mating.

Shell condition was compared between ovigerous and nonovigerous females seasonally using crab pot data combined for all years. Among spring samples, proportionally more nonovigerous than ovigerous females were new-shelled (45% vs. 6%), and proportionally more ovigerous than nonovigerous females were old- (86% vs. 54%) and very old-shelled (8% vs. 1%) (G test, $G = 308.4$, $P < 0.0001$; Fig. 4a). In the fall samples, proportionally more nonovigerous than ovigerous females were soft- (7% vs. 0%) and very old-shelled (21% vs. 10%), and proportionally more ovigerous than nonovigerous females were caught that were new- (31% vs. 26%) and old-shelled (60% vs. 45%) (G test, $G = 7.4$, $P = 0.02$, Fig. 4b). Ovigerous females that were new-shelled in the fall may have molted, mated, hardened, and extruded eggs, whereas old-shelled ovigerous females in the fall probably
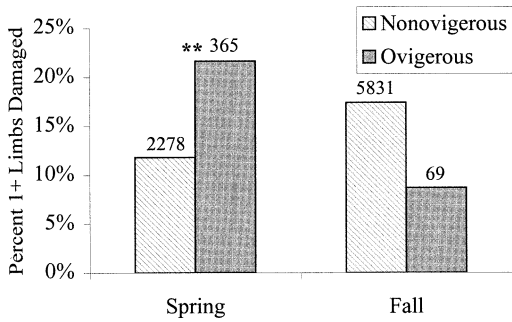
Fig. 3. Comparison of the percentage of ovigerous and nonovigerous female Dungeness crabs for spring and fall samples with one or more appendages damaged. **$P < 0.001$.
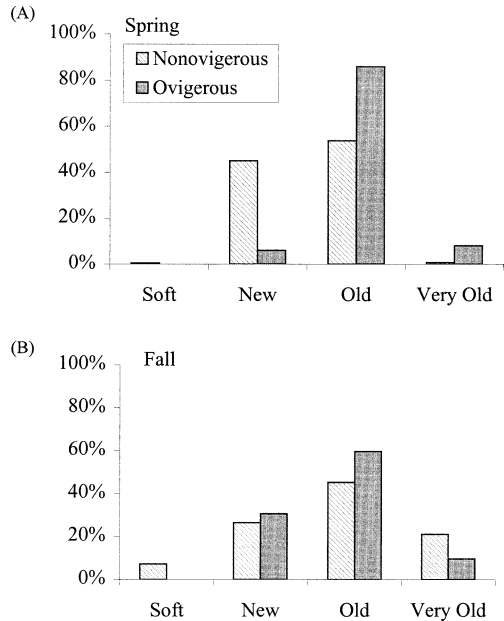

Fig. 4. Percentage of ovigerous and nonovigerous female Dungeness crabs categorized by carapace condition from spring (A) and fall (B) samples. Percentages were based on 2486 nonovigerous and 397 ovigerous females in spring and 6000 nonovigerous and 62 ovigerous females in fall.

relied on stored sperm. The largest proportion of ovigerous females in the fall samples were old-shelled. Examination of ovigerous female shell condition in the fall suggests the majority of females extruding eggs early in the reproductive season were old-shelled.

A total of 16 tagged females were recaptured from the 1739 females tagged and released. Of these 16 recaptures, at least six had not extruded eggs annually (Table 2). At least two females failed to brood eggs in the spring of one year but extruded eggs the following fall. Females that were nonovigerous in the spring were not necessarily senescent but were able to skip a reproductive season and successfully extrude eggs in a following reproductive season. One female extruded eggs in two consecutive years (Table 2). The females that did not molt and extruded eggs probably relied on stored sperm to fertilize their egg clutches. Only three females molted between tagging and recapture (Table 2), confirming that mature (larger) females do not molt yearly. All three crabs that molted increased in carapace width by 15 mm, which is consistent with a single molt for the same size crab using the bent-line growth model presented by Wainwright and Armstrong (1993). In fall samples, three crabs were non-ovigerous when tagged during the crab pot survey. When recaptured by divers a week later, these crabs had extruded eggs, validating that females extrude eggs in September (Table 2).

DISCUSSION

Crab pot and dive data support previous laboratory observations (Swiney and Shirley, 2001) that many mature female Dungeness crabs do not extrude eggs annually in southeastern Alaska. If all mature females extruded eggs annually, there should be few nonovigerous females in our April samples; however 84% of the pot catch and 65% of the crabs encountered on dive transects in April were nonovigerous.

Crab pots preferentially select females that are nonovigerous (Howard, 1982; O'Clair et al., 1990; Taggart et al., in review). We observed this in our study as well. Divers encountered a higher percentage of ovigerous females than crab pots caught (Fig. 1). The difference in capture rates may be attributed to behavioral differences because, compared to nonovigerous females, ovigerous female Dungeness crabs in Alaska bury in the substrate (Stone and O'Clair, 2002), have reduced feeding and foraging responses (Schultz and Shirley, 1997), and may not be as attracted to pots. Furthermore, ovigerous Dungeness crabs in Alaska form dense aggregations (O'Clair et al., 1990; Scheding et al., 2001; Stone and O'Clair, 2001, 2002). If a crab pot is not set close to an aggregation, the chance of collecting ovigerous females is reduced. Likewise, if a dive transect does not happen to intersect an ovigerous female aggregation, the chance of

Table 2. Brief summary and interpretation of data from tagged and recovered female Dungeness crabs ($n = 16$). The presence of blackened pleopods (BP) was evidence of recent egg brooding and no molting. Some individual crabs were represented in more than one row of the table (i.e., six females were nonovigerous in the spring, and one of these females also extruded eggs the following fall, so she is represented in rows 1 and 2). All of the females recovered in this study were not included in this table because clear interpretation of their reproductive histories was not possible. Sp = spring, nonovig = nonovigerous crab, ovig = ovigerous crab, DNB = did not brood.

Reproductive condition and size changes	No. crabs	Interpretation
Sp nonovig	6	DNB that Sp
Sp nonovig; next fall ovig; same size	1	DNB 1 year; extruded following year w/out molting; used stored sperm to fertilize clutch
Sp nonovig; next fall BP; same size	1	DNB 1 year; brooded following year w/out molting; used stored sperm to fertilize clutch
Increase in size between tag and recovery	3	Molted
Sp ovig; next fall ovig; size increase	1	Brooded eggs in 2 consecutive years; molted
Fall pot sampling nonovig; same fall dive sampling ovig; same size	3	Extruded eggs between pot and dive samples

encountering ovigerous females is reduced. Dive transects in this study were not sampled as deep as crab pots were set due to physiological limitation of divers, although the majority of Dungeness crabs brooding aggregations at Glacier Bay are well within the depth range of our dive study. Although our study has some sampling bias, this bias does not mask our observations that not all mature females extrude eggs annually in southeastern Alaska.

Ovigerous females were smaller than nonovigerous females in both the spring and fall, but a greater size difference was observed in the spring samples (Fig. 2). This suggests that larger females are not extruding eggs as frequently as smaller females. Annual molting probabilities for small adult female Dungeness crabs, less than 140 mm CW in California (dependent upon the particular study), are close to one and drop to near zero for females greater than 155 mm CW (Hankin *et al.*, 1989; Mohr and Hankin, 1989; Wainwright and Armstrong, 1993). We assumed that the same trend occurs in Alaska, although the size increments and annual molting probabilities may differ from those occurring at lower latitudes. Our tag and recovery data confirmed that not all mature females molt annually in Alaska, as only 19% of our recoveries had molted. Because larger females do not molt yearly and female Dungeness crabs must molt to mate, these females are probably relying on stored sperm to fertilize their egg clutches. Larger females may then extrude eggs earlier in the reproductive season and be ovigerous during the fall sampling. By the time the spring samples were collected, all of the smaller females that had molted and mated were ovigerous, perhaps explaining the decreased mean carapace width in ovigerous crabs in spring compared to fall. In southeastern Alaska, females that molted prior to egg extrusion did so in June and July (Stone and O'Clair, 2001). Hardening of the carapace requires approximately three months for these females, after which egg extrusion occurs (Shields, 1991); therefore, females would not extrude eggs until September or October at the earliest.

Damaged, missing, or regenerating appendages did not appear to affect the probability of egg extrusion because the occurrence of crabs with missing or regenerating appendages was independent of female reproductive condition. However, a significant difference was detected in the frequency of appendage damage between nonovigerous and ovigerous females caught in the spring. Proportionally, more ovigerous females than nonovigerous females were found with at least one appendage damaged in the spring samples (Fig. 3). The higher proportion of ovigerous females with damaged appendages in the spring may have been the result of damage induced during mating when the female was in a soft-shell state. Butler (1960) discussed mating marks on female Dungeness crabs which result from premating embraces. Damage resulting from courting males and male-male agonistic encounters has been reported for blue crabs, *Callinectes sapidus* Rathbun, 1896 (Smith, 1992). Appendage damage may also have been caused the previous summer, during the commercial fishery, when these crabs were nonovigerous. This would be consistent with the observation that more nonovigerous than ovigerous females were caught in the fall samples with one or more appendages damaged (Fig. 3). Another study in southeastern Alaska

observed more appendage injuries later in the year and hypothesized they may have been the result of molting, mating, or commercial fishing (Shirley and Shirley, 1988).

By examining ovigerous-female shell condition by season, we determined the shell condition of crabs that extruded eggs earlier in the reproductive season (fall samples) and suggested when stored sperm was used to fertilize egg clutches. Our fall sampling was near the beginning of the period of egg extrusion (Shirley et al., 1987; Swiney, 1999; Stone and O'Clair, 2001; Swiney and Shirley, 2001). We found that in September, the majority (60%) of ovigerous females caught were old-shelled and concluded that these females relied on stored sperm and extruded eggs before females that had molted and mated (Fig. 4b). A smaller portion (31%) of ovigerous females in the fall were new-shelled (Fig. 4b). These females probably molted and mated in June or July, as Stone and O'Clair (2001) reported, and extruded eggs prior to our September sampling. In the spring samples, the majority (86%) of ovigerous females were old-shelled (Fig. 4a). This old-shelled group may have comprised females that were classified as old-shelled in the previous fall sampling as well as females that were classified as new-shelled in the fall sampling and reclassified as old-shelled in the spring sampling. The proportions of very old-shelled ovigerous females sampled in the spring and fall were approximately the same (Fig. 4), suggesting that very old females only extrude eggs early in the reproductive season. The ovigerous females that were very old-shelled in both spring and fall used stored sperm to fertilize their egg clutches.

Blackened pleopods, used as an indicator that a female recently brooded eggs without subsequently molting, provided considerable information on the reproductive activity of our tagged crabs. In this study, some females did not extrude eggs for at least one reproductive season. The tag recovery data suggested that some females did not brood eggs in the spring of one year and then extruded eggs the ensuing fall of that year (Table 2). We observed only one female that brooded eggs in two consecutive years, which may be a result of sampling bias against catching ovigerous females. Stone and O'Clair (2002) observed three females of 16 ultrasonically-tagged females that brooded eggs in two consecutive years. Our large nonovig-

erous females do not appear to be senescent but relied on stored sperm to fertilize an egg clutch, even after skipping at least one reproductive season.

We suggest a large number of nonovigerous females were encountered in the spring samples (Fig. 1) because many mature females do not extrude eggs annually in Alaska, which corroborates an earlier laboratory study (Swiney and Shirley, 2001). Gonadosomatic indexes (GSI) were found to be significantly lower among females that extruded eggs when compared to females that did not extrude eggs. Furthermore, GSI and oocyte area of ovigerous females did not increase until after egg hatching (Swiney and Shirley, 2001). Ovigerous females may not have the energy reserves to develop gonads until after egg hatching, due to the reduced feeding and foraging behavior of ovigerous crabs (Schultz and Shirley, 1997) and longer egg incubation periods at colder temperatures (Shirley et al., 1987). Females may not have enough time to hatch eggs and then develop mature gonads; therefore, many females skip at least one reproductive season. Alternatively, many large females may not reproduce because they were unable to find mates and were therefore nonovigerous in the spring. Females require mates that are considerably larger than themselves (Butler, 1960; Snow and Neilsen, 1966), and in a system in which males are heavily exploited, larger females may not mate because appropriately large males are rare. Smith and Jamieson (1991) suggested that in British Columbia, due to the degree of exploitation of males and mating dynamics, females greater than 140 mm CW would have difficulty finding a mate. Hankin et al. (1997) examined this hypothesis in northern California and concluded that virtually all molting females, regardless of size, mated even though the exploitation rate of males in the system studied often exceeded ninety percent; the largest females examined were approximately 166 mm CW (Hankin et al., 1997). A small percentage of the females examined in our study were very large and may have been mate-limited. However, it seems unlikely that the large percentages of nonovigerous female Dungeness crabs observed in this study do not reproduce due to a lack of suitable mates.

This in situ study corroborates the previous laboratory study (Swiney and Shirley, 2001) demonstrating nonannual egg extrusion by mature female Dungeness crabs in southeastern

Alaska. Two different reproductive pathways may be followed by Dungeness crabs in Alaska based, in part, on crab size. Larger females tend not to molt and mate annually but, rather, rely on stored sperm, which may result in these females skipping some reproductive seasons. Smaller females tend to molt, mate, and extrude eggs annually. Egg extrusion does not appear to be annual or synchronous (occurs over half a year), but egg hatching appears to be relatively synchronous in southeastern Alaska.

The frequency of reproduction of a species is an interesting biological phenomenon and an important topic to managers of commercially harvested species. This study and the previous laboratory study (Swiney and Shirley, 2001) strongly suggest that some portion of the mature female Dungeness population is not extruding eggs annually. In the future, we would like to determine more precisely what portion of the female population is not extruding eggs annually in southeastern Alaska. One approach for obtaining direct evidence on the frequency of egg extrusion of female Dungeness crabs would be to attach sonic tags, each with a unique aural code and a battery life of 18 months, to ovigerous crabs. This would permit one to follow individual females through 1+ brooding periods to determine what proportion of the tagged group, if any individuals, brood eggs annually. Crabs could be recaptured and retagged to determine the frequency of egg extrusion over longer periods. A disadvantage to this type of study would be the high cost associated with tagging the large number of crabs required.

LITERATURE CITED

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